MOVEMENT AND SEXUAL DIMORPHISM OF THE ENDANGERED HAWAIIAN COOT, (*FULICA ALAI*), ON OAHU

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ABSTRACT

The endangered Hawaiian Coot, *Fulica alai*, is one of only six native waterbird species remaining in the Hawaiian Islands. Most of its population is concentrated in the wetlands of the islands of Kauai and Oahu. Oahu also has the most wetland loss and fragmentation. This study aimed to determine if the species exhibits sexual dimorphism, if shield size of either sex exhibits seasonal variation, and if morphometric measurements could be used to predict sex accurately, as an alternative to molecular sexing. It also sought to determine if wetland loss and fragmentation prevents movement between wetlands and how common intraisland and interisland movements are. Sixty coots were captured from five Oahu wetlands, tagged with neck collars, and standard morphometric measurements and blood samples (for molecular sexing) were taken. Resight data were collected from ten Oahu wetlands from November 2011 to December 2013. The sex ratio was heavily male biased. No morphological character tested differed significantly between the sexes when assessed independently. However, stepwise binary logistic regression indicated tarsus length, bill height, tail length, and wing length in combination differed between the sexes. Shield size of males exhibited a significant declining trend over the year, being larger in males captured during the pre-breeding and breeding season and smaller in those captured during the post-breeding season. Female shield size did not vary significantly among seasons. The accuracy of predicting sex based on regression models of morphometric measurements was insufficient to substitute for molecular sexing. Habitat fragmentation did not preclude movement, intraisland movement was common and even the widest channels between islands did not impede interisland movement. Movement was not associated with sex, wing length or wing loading. Analysis of resight histories indicated encounter probability was lower during the pre-breeding and early breeding seasons than the late and post-breeding seasons.

CHAPTER 1

Sexual Dimorphism and Seasonal Variability of Shield Size in the Hawaiian Coot, *Fulica alai*

ABSTRACT

The endangered Hawaiian Coot, *Fulica alai*, is one of only six extant, native waterbird species remaining in the Hawaiian Islands. This study aimed to determine if it exhibits sexual dimorphism, and if shield size of either sex exhibits seasonal variation. The study also sought to determine if morphometric measurements could be used in the field to predict sex accurately, as an alternative to molecular sexing. Sixty-five Hawaiian Coots were captured at five wetland locations on the island of Oahu. Standard morphometric measurements and blood samples were taken. Molecular sexing was used to determine the sex of 58 of these individuals. The sex ratio was heavily male biased. No morphological character tested differed significantly between the sexes when assessed independently. However, stepwise binary logistic regression followed by discriminant analysis with cross validation indicated that tarsus length, bill height, tail length, and wing length in combination differed between the sexes. Shield size of males exhibited a significant declining trend over the year, being larger in males captured during the pre-breeding and breeding season and smaller in those captured during the post-breeding season. Female shield size did not vary significantly among seasons. During the breeding and pre-breeding season, a similar binary logistic regression model indicated evidence for sexual dimorphism in shield width, shield length, and wing length. However, the accuracy of predicting sex based on

morphometric measurements using either regression model was insufficient for this approach to be considered a viable substitute for molecular sexing.

Keywords: Rallidae, sex ratio, waterbird, morphometrics, shield size, endangered, Hawaii, conservation

INTRODUCTION

The focus of this study was to assess the morphology of the Hawaiian Coot (*Fulica alai*, Hawaiian name *ʻalae keʻokeʻo*) quantitatively and determine if sexual dimorphism in body or shield characters exists in this species. The Hawaiian Coot is one of the least understood of the six remaining extant native Hawaiian waterbird species, all of which are endangered (USFWS 2011). However, it is also the most abundant of these species, with total population averaging around 2,000 individuals on the main Hawaiian Islands, including 500-1,000 birds on Oahu (Reed et al. 2011, USFWS 2011). Population size has increased in recent decades as wetland protection and management efforts have increased (Engilis and Pratt 1993, Reed et al. 2011, Underwood et al. 2013). Few studies have investigated the breeding biology, anatomy, physiology, or life history of this species, probably because it was considered a subspecies of the American Coot (*Fulica americana*) until 1993 (AOU 1993, Pratt and Brisbin 2002). Further research on its biology could improve management of this endangered species as recommended by the Hawaiian Waterbird Recovery Plan (USFWS 2011) and by Pratt and Brisbin (2002).

Hawaiian Coots have a large, bulbous shield above the bill. The shield size is variable and its color may also vary from bright white to cream or even creamy yellow, with a proportion

of the population having a red shield. Previous studies indicated that as few as 1-3 % of the population have a red shield (Engilis and Pratt 1993, USFWS 2011), whereas Pratt and Brisbin (2002) reported 3-16 % have a red shield depending on the location. The red shield may vary from bright cherry red to dark blood red. Rarely, a bright yellow shield, sometimes with a red spot in the middle, has been noted (Pratt and Brisbin 2002, Riggs personal observation). By contrast, the white shields of American Coots are smaller and typically have a small dark reddish-brown callus at the base (Brisbin and Mowbray 2002). The Caribbean Coot (formerly *Fulica caribaea*) has recently been reclassified as a conspecific form of the American Coot with a white shield that lacks the reddish-brown callus (Chesser et al. 2016). Eurasion Coot (*Fulica atra*) shields are all white. The Hawaiian Coot has long been thought to be closely related to the American Coot because of morphological similarities (AOU 1993, Pratt and Brisbin 2002). Phylogenetic analysis has recently shown that the two taxa are sister species (Garcia-R et al. 2014).

The frontal shield of coots is thought to be a sexual character. Gullion (1951) found that male American Coots had enlarged shields that became more engorged when testosterone levels were raised during the pre-breeding and breeding seasons and then decreased in size during the non-breeding season. A similar seasonal pattern of male shield enlargement has been recorded in Eurasian Coots (Visser 1988). Both male and female Hawaiian Coots appear to exhibit similar displays and behaviors, including parental care for the brood and defending the nesting territory. However, displays and behaviors of the Hawaiian Coot have not been as intensively studied as those of the American Coot (Pratt and Brisbin 2002). Although nesting has been recorded in every month, most breeding is generally thought to begin in the early spring and end in the fall (USFWS 2011).

Like many other members of the Rallidae, coots (genus *Fulica*) are not conspicuously sexually dimorphic. However, male Eurasian Coots do have significantly longer wings and larger heads than females (Minias 2015), and in American Coots a combination of morphological measurements (flattened wing length, metatarsus-midtoe with claw length, culmen-shield length, head length, bill width, gape length, and bill height) can be used to sex individuals with near 90 % accuracy (Eddleman and Knopf 1985). The goals of the present study, therefore, were to determine if sexual dimorphism is also present in Hawaiian Coots, and whether individuals can be reliably sexed using morphometric data, or if molecular sexing of individuals, which can be more costly and invasive, is required for accurate sex determination. There have been no studies of seasonal variability in shield size of Hawaiian Coots, although there is evidence for this in the closely related American and Eurasian Coots (Gullion 1951, Visser 1987, Minias 2015). Therefore, this study also sought to test for such variability, with a view to determining whether shield measurements obtained during different seasons might be more predictive of sex.

METHODS

Data Collection

Sixty-four adult Hawaiian Coots and one juvenile were captured and released on the island of Oahu between November 2011 and April 2013 at five wetlands: Hamakua Marsh, Kailua (21°23'23.67"N, 157°44'30.67"W, 6 birds), Kaelepulu Marsh/Enchanted Lake, Kailua (21°22'33.93"N, 157°44'20.70"W, 25), Pouhala Marsh, Waipahu (21°22'33.93"N, 158° 0'19.64"W, 7), James Campbell National Wildlife Refuge (NWR) – Kii Unit, Kahuku

(21°41'7.86"N, 157°57'14.23"W, 23), and Kuilima Wastewater Treatment Plant (WWTP), Kahuku (21°41'41.16"N, 157°59'27.98"W, 2) (Figure 1). At Hamakua, Kaelepulu, and Pouhala Marshes, birds were captured at night from a canoe using a spotlight and hand dip net from edge habitat along emergent vegetation that is mostly divided into breeding territories. At James Campbell NWR, birds were captured during the day using hand triggered, spring loaded whoosh nets baited with corn on grassy berms between wetland ponds where large groups of mostly non-breeding coots congregate to feed and rest. At Kuilima WWTP, funnel cage traps on the ground baited with corn were used.

On capture, tarsus length, tarsus width, bill length, bill width, shield width, shield length, and bill plus shield length were measured using digital calipers. Wing and tail length were measured with a ruler (to the nearest mm). Bird mass was measured with a 1,000 g spring scale. Shield color and presence of molt were also recorded.

Blood samples from the brachial vein in the wing were collected from 57 individuals, placed in buffer solution (2 mM EDTA, 10 mM Tris, 10 mM NaCl) and stored chilled. In one case, molted feathers collected from a coot that molted during handling were used.

Molecular Sexing and Statistical Analysis of Sex Ratio

A few drops of blood in buffer solution were placed onto FTA cards (GE Healthcare Bio-Sciences, Pittsburgh, Pennsylvania, USA) in preparation for transportation at room temperature (Gutierrez-Corchero et al. 2002). The blood and feather samples were sent to Accumetrics/Viaguard for molecular sexing using primers 1237L, 1272H, and GWR2; this multiplex method of sexing differentiates male and female American Coots unambiguously (Ong

and Vellayan 2008, Shizuka and Lyon 2008). The sex ratio was calculated for the entire sample and for each wetland individually. A chi-square goodness-of-fit test was used to determine if the sex ratio differed significantly from 50:50. A chi-square test for association was used to determine if the sex ratio varied significantly by capture method.

Statistical Analysis of Morphometrics

To detect any morphometric difference between males and females in any one measurement, each was analyzed separately using t-tests. Shield variables were compared between white-shielded males and females; the number of red-shielded females was insufficient for separate statistical analysis of red-shielded birds. Shield colors were analyzed separately since it was unknown if measurements varied with shield color.

Shield width and shield length, and their product (to estimate overall shield size), were analyzed in general linear models with sex, ordinal day captured, and their interaction as explanatory variables.

A model was developed and assessed to determine if a combination of morphometric characters could be used to accurately predict an individual bird's sex. Backward and forward stepwise analysis was first used to select a binary logistic regression model. Then discriminant analysis using the same set of predictor variables with internal cross-validation was used to assess its effectiveness. Of the 64 adult birds captured, 38 (28 males, 10 females) were used in the model. The remaining 26 birds were excluded because they had missing data (22) and/or because they were measured by a different handler, which resulted in outlier measurements (5). Sexual dimorphism was first tested without regard to season. Since male shield size varies

seasonally in other coot species, non-shield characters were chosen for initial inclusion in the model. In combination with other characters, differences in bill and leg morphometrics contribute to sexual dimorphism in the closely related American Coot (Eddleman and Knopf 1985). Therefore, bill width, bill length, bill height, and tarsus length were included in the model at the start of the stepwise procedure. The analysis then assessed these and the following additional variables for inclusion in the model in a stepwise fashion: bill + shield length, shield width, wing length (natural arc), tarsus width, tail length, and bird mass. During this process the initial variables could be removed from the model. An α of 0.15 was used to determine whether variables would be added to or removed from the model. Discriminant analysis with cross validation (Dechaume-Moncharmont et al. 2011) was then performed to determine the accuracy of sex prediction using the morphometric measurements selected by the stepwise binary logistic model.

A similar analysis was performed on morphometric measurements of individuals captured during only the pre-breeding (January-February) and breeding (March-September) seasons (17 males, 8 females) to determine if sex could be more accurately predicted during those seasons. In this case, under the presumption that shield size would vary seasonally, the variables included in the initial stepwise model emphasized shield measurements (shield length, shield width, bill + shield length, and tarsus length). The analysis then assessed these variables as well as bill length, bill width, bill height, wing length (natural arc), tarsus width, bird mass, and tail length, with an α of 0.15 required for entry into or removal from the model. Discriminant analysis with cross validation was then performed using the morphometric measurements selected for inclusion in the model to test the accuracy of sex prediction using the selected characters for birds in the pre-breeding and breeding seasons.

RESULTS

Molecular Sexing and Sex Ratio

Molecular sexing determined sex unambiguously for all adult birds analyzed. Of the 56 birds sexed, 39 were male and 17 female. This differed significantly from the expected 50:50 ratio (chi-square goodness of fit test: $\chi^2 = 8.64$, DF = 1, $p = 0.003$). The sex ratio did not differ by capture method, as the sex ratios at James Campbell NWR (10 males, 8 females) and Kaelepulu Marsh (17 males, 7 females), where markedly different capture methods were used and where sufficient birds were captured to permit statistical analysis, were not significantly different (Pearson chi-square: $\chi^2 = 1.05$, DF = 1, $p = 0.31$). Similarly, there was no significant difference between the sex ratio of all birds captured by night-lighting (28 males, 8 females) and the sex ratio of the James Campbell NWR birds, where baited whoosh-netting during the day was used (Pearson chi-square = 2.84, DF = 1, $p = 0.09$)

Morphometric Variation by Sex and Time of Year

There were no statistically significant differences between males and females (red- and white-shielded coots analyzed together) in any single morphometric measurement (Table 1) or in mean mass (Table 2). However, white shielded females had significantly wider shields than white shielded males (Table 1). The small number of red-shielded coots (11 birds) precluded statistical analysis of differences between red-shielded males and females.

In the general linear model analyzing temporal trends in male and female shield variables, the interaction term was statistically significant for all three variables (shield length, width, and length x width), indicating that trends differed between the sexes (Table 3). Shield size decreased over time in males, but increased slightly in females (Table 4). Males caught during the pre-breeding season (January-February) tended to have larger shields than those caught during the post-breeding season (October-December) (Figure 2). Shield width and length exhibited similar trends to each other across seasons as well as a similar trend to overall shield size (Table 4).

Morphometric Sexing of Hawaiian Coots

The stepwise discriminant analysis using observations regardless of time of year indicated that a binary logistic regression model combining bill height, wing length, tarsus length, and tail length could be used to predict an individual's sex. The regression equation is:

$P(\text{male}) = \exp(Y')/(1 + \exp(Y'))$,

where

$Y' = -6.9 + 2.67$ bill height $+ 0.0875$ wing length $- 0.991$ tarsus length $+ 0.351$ tail length.

Discriminant analysis on the 40 adults (29 males, 11 females) for which there were measurements of bill height, wing length, tarsus length, and tail length indicated that these four measurements could be used to predict the sex of individuals with 77.5 % accuracy using the observed sex ratio of 0.725:0.275. However, after cross-validation this was reduced to 67.5 % accuracy.

The analysis using only birds captured and measured during the pre-breeding and breeding seasons indicated that a binary logistic regression model combining shield length, shield width, and wing length could be used to predict the sex of an individual during the breeding and pre-breeding season. The regression equation is:

P(male) = exp(Y')/(1 + exp(Y')),

where

Y' = -43.0 + 1.832 shield length - 1.193 shield width + 0.1165 wing length.

Discriminant analysis on the 28 adults (19 males, 9 females) for which there were measurements of shield length, shield width, and wing length during the breeding and pre-breeding season indicated that these three measurements could be used to predict the sex of individuals with 78.6 % accuracy using the observed sex ratio of 0.679:0.321. However, after cross-validation this dropped to 67.9 %.

DISCUSSION

The heavily male biased sex ratio is perhaps the most noteworthy and unanticipated finding of this study. A significantly male skewed sex ratio could limit population growth and recovery of this endangered species. This finding is not related to sampling location or capture method. It did not differ significantly between Kaelepulu Marsh and James Campbell NWR, the two wetlands with sample sizes sufficient for statistical comparison. Different methods were used to capture coots at these two wetlands (see Methods) and different management approaches have been adopted at the two wetlands, as follows. James Campbell NWR is considered a core wetland managed by the USFWS with extensive predator control, vegetation management, and

water manipulation to optimize habitat for waterbirds (USFWS 2011). By contrast, the smaller and privately owned Kaelepulu Marsh is classified as a supporting wetland, and lacks the resources to optimize wetland habitat on a large scale (USFWS 2011). All wetlands had a male biased sex ratio, although the sex ratio at James Campbell NWR appeared to be less male biased than at others. However, when the sex ratios of all wetlands where the night-lighting capture method was used (Hamakua, Pouhala, and Kaelepulu) were compared with the sex ratio of James Campbell NWR using a chi-square test, there was no significant difference.

While Hawaiian Coots do not appear to be sexual dimorphic in any single morphological character, a combination of characters provided clear evidence for some degree of sexual dimorphism. Using a binary logistic regression model and stepwise discriminant analysis with cross validation the non-shield characters of bill height, wing length, tarsus length, and tail length could be used to correctly determine the sex of Hawaiian Coots 67.5 % of the time. Sexual dimorphism in these characters involves similar characters to those exhibiting sexual dimorphism in Eurasian and American Coots, which included wing length in the Eurasian Coot (Minias 2015) and wing length and bill measurements in the American Coot (Eddleman and Knopf 1985). American Coot males may be somewhat heavier than females (Alisauskus 1987), but we found no evidence of this in Hawaiian Coots. While our model demonstrates that there is sexual dimorphism, it does not have the accuracy needed to predict sex reliably when compared to the reliability of molecular sexing methods.

A seasonal trend in shield size was observed. Males captured during the pre-breeding and breeding seasons had larger shields than those captured during the post-breeding season, whereas female shield size did not vary with season. This seasonal pattern in shield size change was similar to previously recorded trends in shield size of both American and Eurasian Coots

(Gullion 1951, Visser 1987). The observed seasonal trend of larger, more engorged male shields in the competitive pre-breeding season lends support to the hypothesis that the coot shield is a sexual character. Individuals are competing for mates and establishing and defending nesting territories during the pre-breeding and breeding season. Shield size is influenced by testosterone levels in other members of the Rallidae, and higher testosterone levels cause larger shields (Gullion 1951, Eens et al. 2000). Therefore, Hawaiian Coot males probably have higher levels of testosterone during the pre-breeding and breeding season. Large shield sizes are thought to indicate higher quality and possibly that the males are older. Testosterone has an immunosuppressive effect in other bird species (Hamilton and Zuk 1982). As larger shields result from higher testosterone levels, they may signal to potential mates that these males are able to withstand the immunosuppressive effect. Therefore, individuals with larger shields may have higher reproductive success, and may also be able to defend larger, higher quality territories (Eens et al. 2000, Gullion 1951, Hamilton and Zuk 1982).

Pratt and Brisbin (2002) reported that the proportion of red shielded Hawaiian Coots in the overall population was 3-16 %. In the present study 18 % of coots had red shields. Though only slightly higher than the upper bound of the range estimated by Pratt and Brisbin (2002), this may be evidence that red shields are becoming more common in the population.

The small number of coots with red shields (n=11) precluded statistical analysis of shield differences between red-shielded males and females. The largest shield sizes observed in this study were those of male red shielded coots in the pre-breeding season, but the low number of red shielded males did not permit speculation on the significance, if any, of this observation. However, there were enough white shielded coots to compare shield measurements between the sexes statistically. When compared without consideration of season, white shielded females had

significantly wider shields than males, but this was probably because more white shielded males were captured and measured during the post-breeding season when male shields were smaller.

By developing a model incorporating these shield size variables for the two sexes in the pre-breeding and breeding season, sex was predicted no more accurately (67.9 %) than the model using non-shield characters over the entire year (67.5 % accuracy). While both models provided evidence for sexual dimorphism, neither proved reliable enough in predicting the sex of an individual to replace the essentially 100 % accuracy of molecular sexing. Therefore, in future studies of Hawaiian Coots, we recommend that molecular sexing be used.

In conclusion, this study provided evidence for sexual dimorphism in the Hawaiian Coot, differing seasonal trends in shield size between the sexes, and a heavily male biased sex ratio. These findings should prove useful to conservation of this endangered species and future research on its breeding biology.

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FIGURES

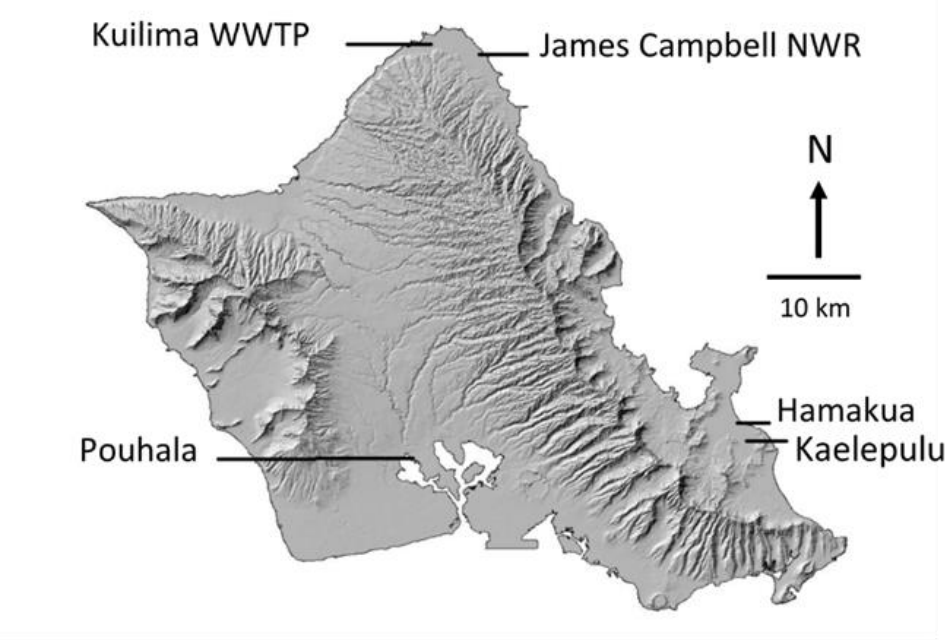

Figure 1. Locations of wetland sites on the island of Oahu where Hawaiian Coots were captured

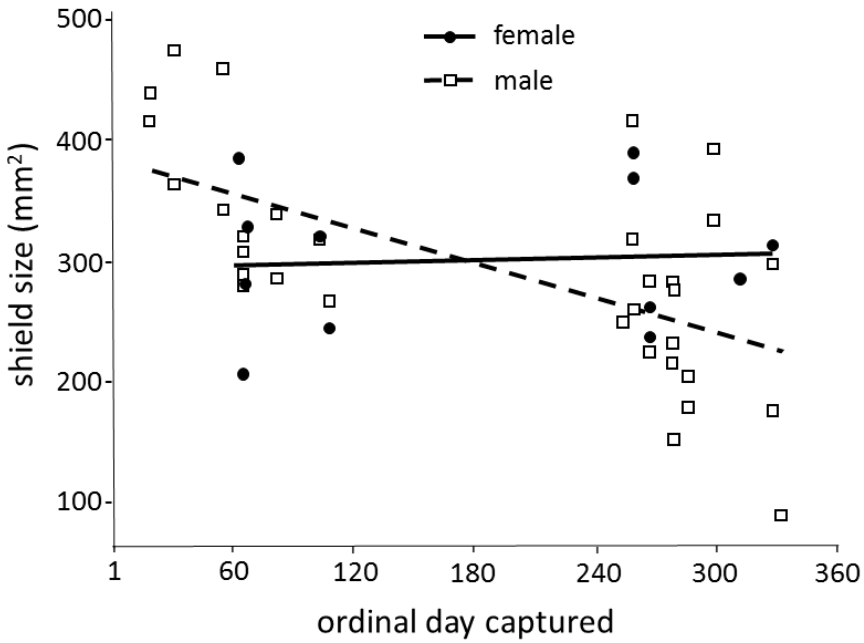

Figure 2. Shield size (mm^2) of Hawaiian Coot males and females by ordinal day captured.

TABLES

Table 1. Comparison (t-tests) of morphometric measurements of male and female Hawaiian Coots. SD, standard deviation; DF, degrees of freedom.

Character	sex	N	Mean (mm)	SD	*P*-value	DF
Wing length					0.98	25
	female	14	181.5	9.2		
	male	35	181.4	9.79		
Tarsus length					0.056	34
	female	16	57.4	3.47		
	male	37	55.2	4.28		
Shield length					0.35	30
	female	14	22.1	2.63		
	male	36	21.25	3.38		
Bill + shield length					0.41	42
	female	16	54.01	2.76		
	male	38	53.2	4.27		
Shield width					0.51	28
	female	16	13.98	2.27		
	male	38	13.52	2.3		
Shield length (white shields)					0.11	21
	female	11	22.54	2.66		
	male	31	20.89	3.31		
Shield width (white shields)					0.03	25
	female	11	14.55	1.5		
	male	32	13.19	2.16		

Table 2. T-test comparison of male and female Hawaiian Coot mass.

	N	Mean (g)	SD	*p*-value	DF
Males	39	549	87.5		
Females	16	557	54.0	0.69	44

Table 3. Regression statistics for shield size (length x width), shield width and shield length of male and female Hawaiian Coots, January to December.

		Length x width	Width	Length
Source	DF	*p*-value	*p*-value	*p*-value
Model	3	0.001	0.01	< 0.001
Date	1	0.81	0.71	0.33
Sex	1	0.02	0.048	0.002
Date*sex	1	0.02	0.048	0.002

Table 4. Slope of regressions of shield measurements, January to December.

	Length x width	Width	Length
Males	- 0.469	- 0.01036	- 0.01894
Females	+ 0.046	+ 0.00195	+ 0.00678

CHAPTER 2

Movement and Encounter Probability of the Endangered Hawaiian Coot, *Fulica alai,* in the Fragmented Wetland Landscape of Oahu, Hawaii

ABSTRACT

The endangered Hawaiian Coot (*Fulica alai*) is endemic to the main Hawaiian Islands, with most of its population concentrated in the coastal wetlands of the islands of Kauai, Oahu and Maui. Oahu, the island with the second largest numbers of coots, also has the most wetland loss and fragmentation. Intraisland movements of coots between the remaining wetlands and rarely, interisland movements, have been observed. However, little is known about how common such movements are or what influences them. This study aimed to determine if wetland loss and fragmentation prevents movement between wetlands and how common intraisland and interisland movements are. Sixty coots were captured from five Oahu wetlands and tagged with uniquely marked neck collars. Resight data were collected from ten Oahu wetlands from November 2011 to December 2013. Of the coots collared, 11 moved intraisland and three interisland (to Kauai and Molokai); another 20 probably moved to another wetland as they were not resighted at the wetland where they were tagged for five consecutive months or more. Thus, habitat fragmentation does not preclude movement, intraisland movement is common and even the widest channels between islands do not impede interisland movement. Movement was not associated with sex, wing length or wing loading. Analysis in Program MARK of resight histories at Kaelepulu, the wetland with the largest sample size and longest period of resight surveys, indicated encounter/resight probability was lower during January–June (pre-breeding

and early breeding season) than July–December (late and post-breeding season). Increased movement to other wetlands in the pre-breeding and early breeding season may be due to birds searching for mates or suitable breeding territory. The MARK analysis supports the hypothesis that coot movements are more associated with reproduction and breeding than with the rainy season (as suggested by some previous studies).

Keywords: Rallidae, waterbird, conservation, collar, mark-resight, Program MARK

INTRODUCTION

The endangered Hawaiian Coot (*Fulica alai*) is one of the least understood of the five endemic Hawaiian waterbird species that remain extant in the main Hawaiian Islands (USFWS 2011). While numbers of individuals at large, managed National Wildlife Refuges are stable and perhaps increasing slightly, populations at smaller wetlands and those that lack intensive management have shown more fluctuation (USFWS 2011). Intensive management of this species, which is deemed 'conservation reliant', and protection of its habitat have been necessary to maintain a stable population (Reed et al. 2011, Underwood et al. 2013).

An estimated 1,500 to 2,000 Hawaiian Coots remain (Underwood et al. 2013), but the factors influencing the population fluctuations have not been studied comprehensively (USFWS 2011), and further research has been recommended by Pratt and Brisbin (2002) and by the Hawaiian Waterbird Recovery Plan (USFWS 2011). Changes in population size may be due to movement to and from smaller wetlands that are not included in census data, or to variable reproductive success (USFWS 2011).

Hawaiian Coots occupy a fragmented mosaic of habitat islands within the Islands. For example, formerly extensive wetland habitat on the island of Oahu has been reduced by 65 % and fragmented by urban development and drainage for agriculture (Van Rees and Reed 2014). As suggested by the Hawaii Waterbird Recovery Plan (USFWS 2011), studies are needed to understand the movements of Hawaiian Coots in this fragmented habitat to improve management strategies. Frequent population fluctuations have been noted in several studies (Udvardy 1960, Engilis and Pratt 1993, USFWS 2011, Reed et al. 2011, Pratt 1978, 1987). However, populations at intensively managed wetlands have been more stable and have increased in recent years (Reed et. al 2011, 2012, Underwood et al. 2013). Coots may move to ephemeral wetlands after heavy rains, and such movements are known to occur between the islands of Kauai and Niihau (USFWS 2011). At Salt Lake and Kaelepulu Pond (Oahu), formerly large wetlands, frequent fluctuations in numbers corresponded to seasonal changes in water levels and were thought to be the result of movement from other wetlands or islands (Udvardy 1960).

Waterbird survey data from 1977 to 1987 were interpreted by Engilis and Pratt (1993) as indicating that survey counts of Hawaiian Coots were inversely related to rainfall. This trend was observed simultaneously on all islands and was thought to be the result of coot movement from larger surveyed wetlands to ephemeral, unsurveyed wetlands that provided suitable habitat only during wet periods. However, Engilis and Pratt (1993) used rainfall data from only one weather station as an approximation for all islands and only had reliable survey data from ten years. When survey data from several decades were analyzed with island specific rainfall, no correlation between rainfall and numbers was found (Reed et al. 2011). The fluctuations must therefore be related to other, unknown factors, perhaps food availability, wetland salinity or reproduction.

Coots are poor fliers compared to some waterbird species because of their relatively shorter wings, and only fly at night, which contributes to the difficulty in observing movement events (Rosser 1980). Also, with the exception of coots marked with neck collars on Molokai since 2007, and a movement study that ended in 1992 by the Hawaii State Department of Fish and Wildlife using turkey leg bands as neck collars (Dibben-Young 2010), they have typically been banded only with an aluminum Fish and Wildlife Service band. At some federally managed wetlands they have also been marked with colored leg bands corresponding to the wetland in which they were captured. To track individual movements, recapture has therefore usually been required.

Coots may depend on small remnant wetlands as stopover sites when moving between larger wetlands or those with more suitable breeding habitat. Wetlands are now separated by large tracts of development and agriculture where nearly continuous wetlands once existed, notably at lower elevations along the coasts. Developed areas may act as barriers to movement and effectively fragment the overall population. Since mountains may also be barriers to movement, loss of these wetlands could separate populations on the opposite sides of a mountain range that were formerly connected via essentially contiguous coastal wetland habitat. Although the ocean channels between islands presumably constitute a major barrier, banding studies have provided evidence of some inter-island movement. Prior to this study, a bird banded on Oahu was resighted on Molokai, and a bird collared on Molokai was resighted on Maui and subsequently again on Molokai (Dibben-Young 2010).

This study aimed to answer two main questions to improve understanding of Hawaiian Coot movements and population connectivity. First, what proportion of the population moves between wetlands and between islands: (a) does habitat fragmentation prevent coot movement

between wetlands, and (b) how common is intraisland movement on Oahu and interisland movement from Oahu? Second, what factors influence coot movements: (a) is movement sex biased, (b) is movement associated with longer wing lengths or wing loading, and (c) does movement (inferred by encounter/resight probability and apparent monthly survival probability) vary with time of year and/or sex.

The results should inform natural resource managers and biologists making decisions to manage the species as a single population or to manage populations by island or wetland, depending on the levels of connectivity among wetlands. Improved knowledge of the movements of this species within a significantly reduced and fragmented wetland landscape may more generally help improve management strategies for other endangered Hawaiian waterbirds and the wetlands on which they depend.

METHODS

This study adopted mark-resight methodology using conspicuous markers (plastic Darvic® neck collars and USFWS aluminum leg bands). Collars were yellow with black three-letter digit codes repeated twice around the collar following the style used by Dibben-Young (2010). Sixty adult coots were captured, collared and released on Oahu between November 2011 and April 2013 at five wetlands: Hamakua Marsh, Kailua (21°23'23.67"N, 157°44'30.67"W, 6 birds), Kaelepulu Marsh/Enchanted Lake, Kailua (21°22'33.93"N, 157°44'20.70"W, 24), Pouhala Marsh, Waipahu (21°22'33.93"N, 158° 0'19.64"W, 7), James Campbell National Wildlife Refuge (NWR) – Kii Unit, Kahuku (21°41'7.86"N, 157°57'14.23"W, 21), and Kuilima Wastewater Treatment Plant (WWTP), Kahuku (21°41'41.16"N, 157°59'27.98"W, 2) (Figure 1). Capture

techniques included baited hand triggered, spring loaded ground whoosh nets at James Campbell NWR, baited funnel cage traps at Kuilima WWTP and night lighting with hand nets at Hamakua, Kaelepulu and Pouhala Marshes.

On capture, wing length was measured with a ruler (to the nearest mm). Blood samples from the brachial vein in the wing were collected and stored in buffer solution. In one case, molted feathers collected from a coot that molted during handling were used. Blood and feather samples were sent to Accumetrics/Viaguard for molecular sexing using primers 1237L, 1272H and GWR2; this multiplex method of sexing differentiates male and female American Coots unambiguously (Ong and Vellayan 2008, Shizuka and Lyon 2008)

In addition to frequent resight surveys (1-3 per month) at the five wetlands where coots were captured, other wetlands were surveyed opportunistically for collared coots (Figure 1). Flyers informing biologists, natural resource managers and the birding community were also sent out in an attempt to increase the number of resights on Oahu, as well as on other islands in case of interisland movement. Birds were resighted using binoculars and spotting scopes. The Hawaiian Coot is one of the more conspicuousness species in these habitats and favors open water, which allows for high resight probabilities (Underwood et al. 2013).

Each bird was classified into one of six movement categories based on resight data: (1) not resighted, (2) probably moved (resighted, but not seen for five or more months consecutively), (3) probably resident (consistently resighted at the wetland where it was tagged with no non-sighting for more than three consecutive months) (4), short intraisland movement (1 – 5 km), (5) long intraisland movement (15 – 45 km) and (6) interisland movement. One coot at James Campbell NWR could not be categorized because its decayed carcass was found at the NWR two months after capture. A chi-square test was used to test for an association between sex

and movement by comparing coots considered probably resident (category 3) with those that probably moved and were known to have moved (categories 2 and 4-6).

To test if movement was associated with longer wing length and/or wing loading (estimated as bird mass/wing length), mean wing length and mean wing loading were compared between the same categories as above for sex.

Sample sizes of coots marked with neck collars at two wetlands, James Campbell NWR and Kaelepulu Wetland/Enchanted Lake, were sufficient for further analysis of resight data in Program MARK (White and Burnham 1999), using Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965). These analyses were used to estimate (1) apparent monthly survival probability (φ), which is the probability that a collared coot in the study population at the wetland where it was captured survived from one resight period (month) to the next, and remained in that wetland (did not permanently emigrate), and (2) resight/encounter probability (*p*), which is the probability that a collared coot in the study population at the wetland where it was captured was resighted during a given month. Both φ and *p* can be used to infer movement out of a study population. At Kaelepulu Marsh 64 resight surveys were conducted from January 2012 to November 2013 and pooled into 21 monthly encounter occasions (no surveys December 2012 and February 2013) for input into Program MARK for 23 individuals of known sex (Appendix Table A1). At James Campbell NWR 34 resight surveys were conducted from November 2012 to December 2013 and pooled into 13 monthly encounter occasions (no surveys April 2013) for the 14 sexed individuals (Appendix Table A2). Two coots that died were excluded from the input data as the CJS model does not allow for known deaths. Five coots were excluded from the James Campbell NWR analysis because blood or feather samples were not collected for sexing.

Aikake's information criterion was used to test whether apparent monthly survival (φ) or resight probability (*p*) varied significantly with season or sex, and to select the model that best fit the resight data at each wetland analyzed. The following models were assessed: φ.*p.* which represents constant apparent monthly survival probability (φ) and constant resight probability (*p*); φ(sex).*p*. and φ(wetdry).*p*. in which φ varied respectively with sex and wet/dry season (the wet season is October – April); and φ.*p*(sex)., φ.*p*(wetdry). and φ.*p*(breeding). in which *p* varied respectively with sex, wet/dry season and breeding season (the pre-breeding and early breeding season is January – June).

RESULTS

Twenty-three collared coots (38 %) were probable residents of the wetland where they were captured as they were resighted at that wetland throughout the study and not at any other wetland; 20 (33 %) probably moved to another wetland, but were not resighted as such; and 13 (22 %) were recorded in a wetland other than the one where they were originally captured (Table 1). There were 24 total recorded instances of movement, as some birds moved intraisland multiple times (see Appendix Table A3 for resight records of birds that moved multiple times). In four instances of intraisland movement a bird would have either crossed a mountain range or flown around it (Figure 2). Two individuals moved from Oahu to Kauai (Table 1) and one moved from Oahu to Molokai, but it could not be identified as it was too far away to read the three-letter code on its collar and determine its wetland of origin. One collared coot was seen at Nuupia Ponds, but was also too far away to read the code.

Of the coots that were sexed, 21 were probable residents (6 females, 15 males) and 30 either moved or probably moved (8 females, 22 males); movement was not significantly associated with sex (χ^2 = 0.023, DF = 1, p = 0.881). Of birds with measured wing lengths, 20 were probable residents (mean and standard deviation of wing length, 181.75 ± 9.08 mm) and 28 either moved or probably moved (180.63 ± 9.15 mm); mean wing length did not differ significantly between the two groups (t-test, DF = 41, p = 0.675). Mean wing loading also did not differ significantly between the two groups (probable residents, 3.053± 0.342 g/mm; moved or probably moved, 3.012 ± 0.452; t-test, DF = 45, p = 0.725).

At Kaelepulu Marsh, Program MARK indicated that, of the models tested, the φ.*p*(*breeding*). model had the most support (AICc weight = 0.698) followed by the φ.*p*(*wetdry*). model (AICc weight = 0.2989) (Table 2). At JCNWR, the φ.*p* model had the most support (AICc weight = 0.3020) followed by the φ.*p*(*wetdry*). (AICc weight = 0.2371) and φ.*p*(*sex*). (AICc weight = 0.1542) models (Table 3).

The best fit models for each wetland indicated apparent monthly survival probability did not vary by time of year or sex (James Campbell NWR, 0.94 ± 0.025; Kaelepulu, 0.96 ± 0.013). The monthly encounter/resight probability according to the best fit model for the James Campbell NWR data was also constant (0.631 ± 0.059). However, at Kaelepulu the best fit model indicated the monthly resight probability was lower during January – June (the pre-breeding and early breeding season; resight probability, 0.434 ± 0.053) than during July – December (the late and post breeding season; 0.698 ± 0.043).

DISCUSSION

This study shows that Hawaiian Coots move within and between islands. Despite the significant reduction of wetland habitat on Oahu, neither mountain ranges nor large tracts of developed land appear to be significant barriers to movement. Most of the movements occurred within the very urbanized landscape around Pearl Harbor and the heavily developed suburban landscape of the Kailua area on the eastern side of Oahu. Furthermore, even the largest channel between two of the main Hawaiian Islands, Oahu and Kauai, does not appear to be a significant barrier to interisland movement. This is the longest distance a Hawaiian Coot has been recorded moving, and is the first record of movement between Kauai and Oahu. Coots are clearly able to move between wetlands, despite extensive habitat loss on Oahu, and as such it is expected that they would not exhibit significant population structure. There was no evidence of movement being associated with sex, wing length or wing loading.

The models with the most support indicated apparent monthly survival probability (φ) at both Kaelepulu and James Campbell NWR remained constant across seasons and regardless of sex, with approximately a 6 % monthly loss of collared coots from the James Campbell NWR site and 4 % monthly loss from the Kaelepulu site. These percentages reflect birds that were not seen again during the duration of the study at the wetland where they were captured, but some were resighted at other wetlands. The best fit model of the Kaelepulu wetland resight data indicated that encounter/resight probability in the pre-breeding and early breeding season (January – June) is lower than that during the late and post-breeding season (July – December). This difference could be the result of movement to other wetlands in the pre-breeding and early breeding season when birds may be searching for mates or suitable breeding territory. For

instance, males could be moving more during the early pre-breeding season, searching for suitable territories, and later unpaired females may move between wetlands as they look for males with established territories. The variation could also be related to differences in food availability, water levels or salinity at different times of the year. The best supported model at James Campbell NWR indicated resight probability remained constant across months. However, the sample size was smaller and the duration of resight surveys was shorter than at Kaelepulu, which may have limited the ability to detect seasonal differences. Although Engilis and Pratt (1993) suggested that variation in surveyed population numbers differed between wet and dry seasons, the present study indicated that this was not the case, supporting the conclusion of Reed et al. (2011), based on more rigorous and longer term data, that rainfall was not the driver of variation in counts. Further studies are recommended to determine if the seasonal effect in movement observed at Kaelepulu occurs at other wetlands, and if a combined effect of sex and season occurs.

In conclusion, this study of Hawaiian Coot movement should be of use to managers of the various wetlands. Furthermore, because the study was undertaken at a variety of differently managed and owned wetlands (private, state, federal), this suggests collaboration in management planning and sharing of information regarding changes in surveyed population size will be especially important for conservation of Hawaiian Coots and other endangered waterbirds and for the management of their habitat.

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FIGURES

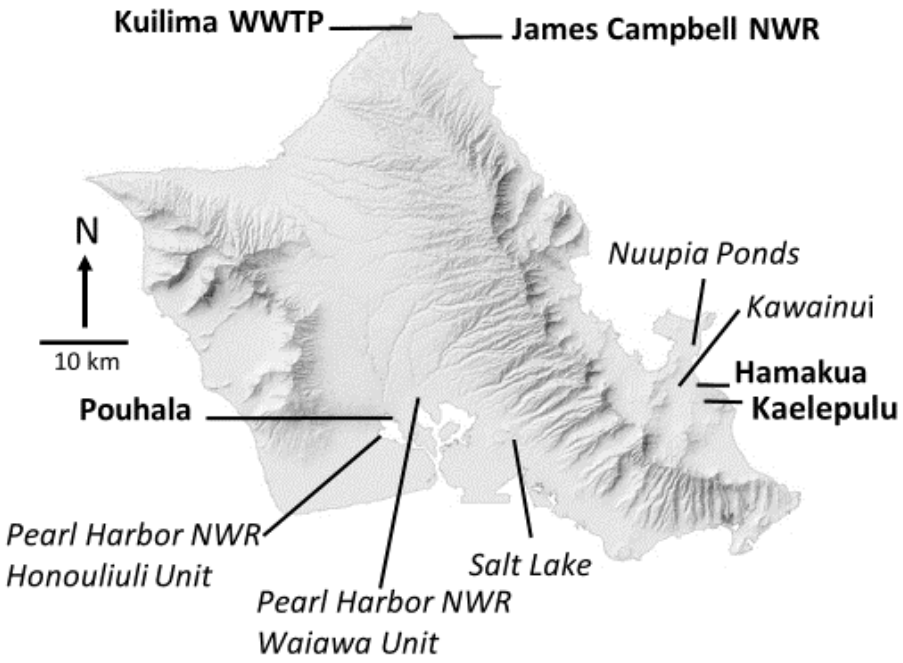

Figure 1. Locations of wetland sites on the island of Oahu. Bold font – wetlands where coots were captured and resighted; italic font - wetlands where only resight surveys were conducted.

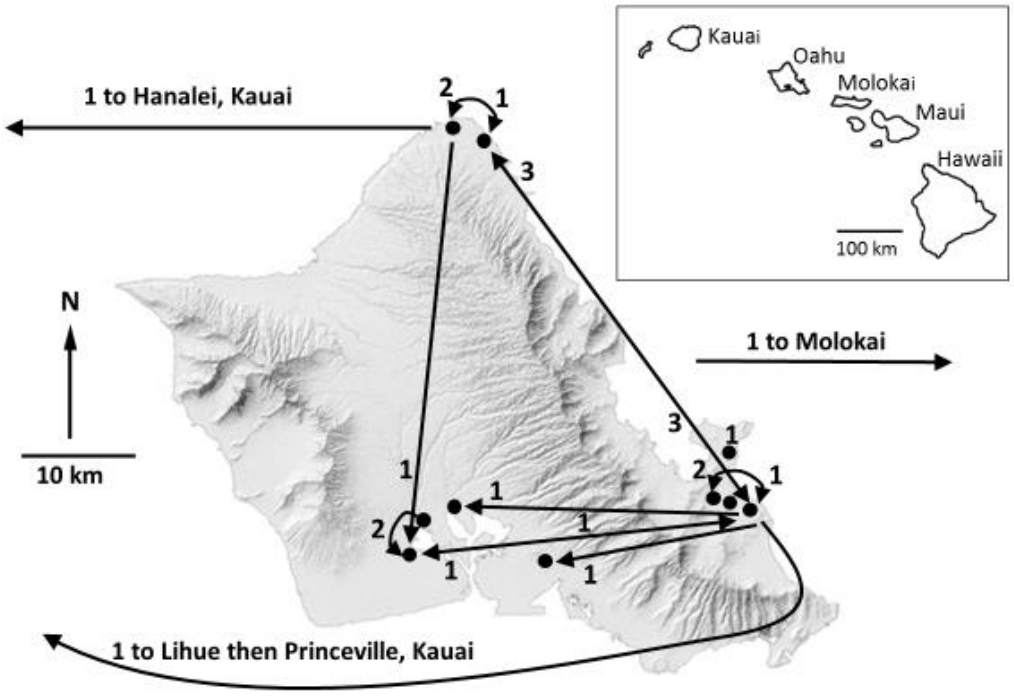

Figure 2. Intraisland and interisland movements recorded on and from Oahu, November 2011 – December 2013. Numbers reflect instances of movement, with numbers closer to the arrowheads indicating movement in that direction.

TABLES

Table 1. Resightings of Hawaiian Coots collared at five wetlands on Oahu, November 2011 – December 2013.

Wetland where captured	n	Died, movement unknown	Not resighted	Probably moved	Probably resident	Short intraisland movement	Long intraisland movement	Interisland movement
Hamakua	6	0	0	2	4	0	0	0
Kaelepulu	24	0	1	9	8	2	3	1
Pouhala	7	0	0	3	2	2	0	0
JCNWR	21	1	2	6	9	2	1	0
Kuilima WWTP	2	0	0	0	0	0	1	1
Total	60	1	3	20	23	6	5	2*

* does not include the single unidentified coot that moved from Oahu to Molokai

Table 2. Comparison of models in Program MARK with variation in encounter probability (*p*) and apparent monthly survival probability (φ) by season and sex for Hawaiian Coots at Kaelepulu Marsh (n = 22). No. Par. – number of parameters in the model.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
ϕ.*p*(*breeding*).	361.56	0.00	0.6898	1.0000	3	305.12
ϕ.*p*(*wetdry*).	363.23	1.67	0.2989	0.4333	3	306.80
ϕ.*p*(*sex*).	370.66	9.10	0.0073	0.0106	3	314.23
ϕ.*p*.	373.03	11.47	0.0022	0.0032	2	318.67
ϕ(*wetdry*).*p*.	374.71	13.15	0.0010	0.0014	3	318.28
ϕ(*sex*).*p*.	375.09	13.53	0.0008	0.0011	3	318.66

Table 3. Comparison of models in Program MARK with variation in encounter probability (*p*) and apparent monthly survival probability (φ) by season and sex for Hawaiian Coots at James Campbell NWR (n = 14). No. Par. – number of parameters in the model.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
ϕ.*p*.	140.61	0.00	0.3020	1.0000	2	93.05
ϕ.*p*(*wetdry*).	141.09	0.48	0.2371	0.7851	3	91.31
ϕ.*p*(*sex*).	141.95	1.34	0.1542	0.5107	3	92.17
ϕ(*sex*).*p*.	142.73	2.12	0.1045	0.3461	3	92.95
ϕ.*p*(*breeding*).	142.77	2.16	0.1026	0.3398	3	92.99
ϕ(*wetdry*).*p*.	142.83	2.22	0.0996	0.3298	3	93.05

APPENDIX

Table A1. Kaelepulu Marsh monthly resight history for sexed birds (n = 23) January 2012 – November 2013; December 2012 and February 2013 excluded. 1, resighted; 0 not resighted.

Individual resight history	Sex
100000000000000000000	M
100100000000000000000	M
011010101101001010001	M
011011111101000000000	M
001011101100000000000	F
001001101000000000000	M
001100000000000000000	M
001100011001001011110	M
000100111111001111100	M
000111001000000000001	M
000111111111101111111	F
000000001111001111110	M
000000001110000011110	M
000000001111001010001	F
000000001111001110001	F
000000001100000000000	M
000000001111001110000	M
000000001111011000000	F
000000001101111111110	M
000000001100000000000	F
000000001110001110100	M
000000000011001111100	M
000000000010000011110	M

Table A2. James Campbell NWR monthly resight history for sexed birds (n = 14) November 2012 – December 2013; April 2013 excluded. 1, resighted; 0 not resighted.

Individual Resight History	Sex
1000000000000	M
0111111111011	M
0000101000000	M
0000111001010	F
0000110001011	M
0000111101000	F
0000110000000	M
0000110111001	M
0000100000000	F
0000101000000	M
0000111111001	F
0000111111011	F
0000100011111	M
0000100011001	M

Table A3. Individuals with multiple recorded movements.

Individual (collar code)	Wetland where captured	Other wetlands where resighted (in chronological order)
AAC	Kaelepulu	Kauai Lagoons (Lihue, Kauai), Princeville Golf Course, (Princeville, Kauai)
AAV	Kaelepulu	James Campbell NWR, Kaelepulu
ABC	Kaelepulu	Kawainui, Kaelepulu
ABN	Kaelepulu	Pearl Harbor NWR Honouliuli Unit, Kaelepulu, Salt Lake
AFB	James Campbell NWR	Kuilima, James Campbell NWR
AFT	James Campbell NWR	Kaelepulu, James Campbell NWR, Kaelepulu, James Campbell NWR